INFORMATION CONTENT OF PREY ODOR PLUMES: WHAT DO FORAGING LEACH'S STORM PETRELS KNOW?

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INTRODUCTION

Electrophysiological responses to odor have been recorded for concentrations as low as 0.01 ppm for Manx Shearwaters *Puffinus puffinus* and Black-footed Albatrosses *Diomedea nigripes*, indicating that relative to most birds, procellariiforms have a keen sense of smell (Wenzel and Sieck 1972, cf. Clark 1991; Clark and Smeraski 1990; Clark and Mason 1989). Such acuity is not unexpected, given the extensive development of the olfactory anatomy of these species (Bang and Wenzel 1986). Field observations indicate that Procellariiformes use their sense of smell to locate food (Grubb 1972; Hutchison and Wenzel 1980; Lequette, Verheyden and Jouventin 1989). However, it is not known how far from the source petrels can detect odors. This information would improve our understanding of procellariiform foraging ecology and engender a broader appreciation of the selective forces involved in shaping the evolution of the sensory anatomy of this group (Healy and Guilford 1990). Herein, we report preliminary observations on the odor sensitivity of Leach's Storm Petrel *Oceanodroma leucorhoa* to the major components of natural prey items. The detection data are used to generate a first order estimate of the odor active space for free ranging petrels.

SENSITIVITY TO ODORS

If the evaporation rate and threshold sensitivity for odorants are known, then odor dispersion models can be used to estimate the active space within which petrels could theoretically detect and use odors to orient toward prey (Bell and Carde 1984). Towards this end we tested odor responding by Leach's Storm Petrels to krill *Euphausia superba* by monitoring changes in cardiac response to volatiles (Shallenberger 1973). The aroma of krill is composed of a variety of components that have distinct odors (at least to humans) (Kubota, Uchida, Kurosawa, Komuro and Kobayashi 1989). Three fractions prepared from a nonpolar extraction of freeze dried krill were tested: carboxylic acids, phenols and amines. To the human observer the carboxylic acid and phenol fractions were essentially odorless while the amine fractions smelled strongly like fish/shrimp. The "fishy" odor of krill is primarily attributable to pyrazines and N,N-dimethyl-2- phenyleth-

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yl amine (Kubota and Kobayashi 1988). The relatively less volatile carboxylic acids contain free fatty acids such as linolenic acid (Kubota and Kobayashi 1988).

Volatiles from each fraction were presented separately to birds via a dilution olfactometer (Clark and Mason 1989). Responsiveness to an unconditioned odor stimulus was defined as a change in heart rate relative to a humidified air control (Wenzel and Sieck 1972; Shallenberger 1973; Clark and Mason 1989). Petrels showed different sensitivity to odors derived from the three extracts (Figure 1). Petrels were most sensitive to amines and least sensitive to the carboxylic acid fraction. In general, the sensitivity probably corresponds to the actual molecular concentration of components evolving from the mixtures (Mozell, Sheehe, Swieck, Kurtz and Hornung 1984). Based upon gas chromatographic/mass spectral analysis of the volatiles derived from krill, the amine fraction contains the more volatile components, while the carboxylic acid fraction contains the least volatile components [Clark, unpublished data].

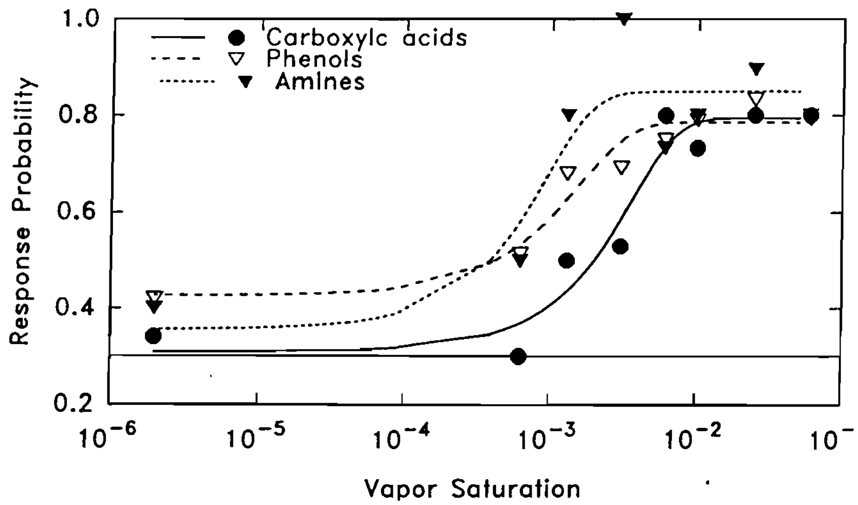

Figure 1. Response probabilities of Leach's Storm Petrels to organically derived odors. The odors represent mixtures of compounds composed primarily of the three specified classes.

RESPONSE TO ODOR FRACTIONS IN THE FIELD

In the field, petrels orient towards a variety of organically derived odors, e.g. cod liver oil, fish homogenate (Hutchison and Wenzel 1980; Lequette et al. 1989). To test how Leach's storm petrels responded to fractions of krill we used military night vision goggles to observe the flight behavior over a breeding colony located at the Bowdoin College Field Station at Kent Island, New Brunswick, Canada.

Leach's storm petrels are only active over land during the night, presumably because of risk of predation from herring *Larus argentatus* and great black-backed *L. marinus* gulls. The attractiveness of odor fractions was patterned after studies done at sea (Grubb 1972; Hutchison and Wenzel 1980; Lequette et al. 1989). Briefly, a 1.5 m high platform was set out

over an open field and homogenates of krill or prepared fractions were placed in 80 mm diameter pans set atop a platform by a second individual. Thus, the observer was blind to the identity of the odor source. Prior to testing with the krill fractions, the procedures and methodology were refined by observing flying patterns in response to commercially available cod liver oil. Five stimuli were tested: a water control, homogenate of krill, extracted fractions of amines, phenols and carboxylic acids. These fractions were prepared in identical fashion as that described for the laboratory threshold studies. Observation periods were for 5 min. An observer hidden behind vegetation watched a 90o area downwind from the platform. During that time counts of all birds passing through the observation field, up to a distance of approximately 100 m (the limit of reliable resolution for the night goggles), were recorded. Birds that passed within about 20 m of the platform, or showed a tight circling pattern around the platform (vide Grubb 1972), were counted as having expressed an interest in the odor source. A 10 minute interobservation period followed to allow for odor dispersal and avoid habituation by birds.

There were differences in attractiveness among the stimuli (Figure 2, F=7.77, df=4,30, P=0.0002). Post-hoc tests showed that petrels were equally attracted to all the organic fractions and whole homogenate. However, only the whole homogenate and the carboxylic acid fraction differed from the blank. Subsequent GC/MS analysis of the stimuli did not reveal any obvious fractions that presented themselves as likely candidates for an attractant. Nonetheless, there appear to be subtle but reliable differences in attractiveness of the different components of krill. Interestingly, the component that to humans is perceived as fishy, is not apparently the cue to which petrels are most strongly attracted. Serial dilutions of the original stock carboxylic acid solution showed that attractiveness was linearly related to log concentration of the stimulus (Figure 3).

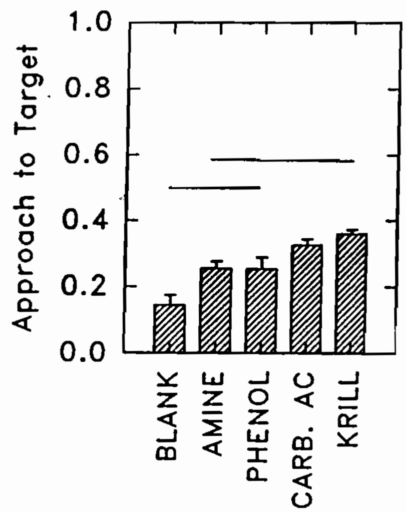

Fig. 2. The proportion of petrels within a visual field that were attracted to the odor target. The horizontal lines indicate homogenous groups based upon a post-hoc test. Vertical bars are + one standard error.

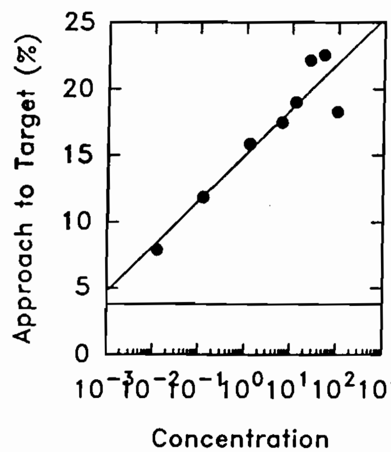

Figure 3. The proportion of petrels within a visual field that were attracted to dilutions of carboxylic acids derived from krill. The horizontal line depicts approaches to the water control.

DISCUSSION

Leach's storm petrels are opportunistic surface feeders. However, the majority of feeding occurs at night (Watanuki 1985). This foraging pattern is consistent with the availability of preferred prey (Brinton 1967; Kawaguchi 1969). For example, E. superba (a major component of petrel diet) generally are near the surface at night, but at a depth of about 100m during the day (Maurano, Marumo, Nemoto and Aizawa 1976; Sekiguchi 1975; Everson 1984). In addition to the temporal variation in availability, prey are distributed patchily and unpredictably, even in areas of uniform physical and chemical oceanographic characteristics (Brown 1980; Everson 1984). Under some conditions petrels may use meteorological anomalies to increase their chances of encountering prey (Brown 1980). Certainly, once in proximity to prey they readily orient using visual cues (Hutchison and Wenzel 1980). However, under low visibility conditions, the only reliable means to survey large tracts of ocean for prey is to use odor cues (Grubb 1972; Hutchison and Wenzel 1980; Lequette et al. 1989; Healy and Guilford 1990). The question remains as to whether this feat is possible on the scale of kilometers (Smith and Paelk 1986; Waldvogel 1987).

We used a three dimensional Gaussian puff model for a continuously generating odor source to model the dispersion pattern of volatile components of krill (Fleischer 1980). For simplicity, we estimated the physical characteristics of a highly volatile amine (pyrazine) and a less volatile fatty acid (linolenic acid) (Reid, Prausnitz and Poling 1986; Kubota et al. 1989). For illustrative purposes, we assumed atmospheric conditions to be neutrally stable, ocean and air temperature to be $10^{o}C$, wind speed to be 5 m/s, the inversion layer to be 10,000 m elevation, no cloud cover, and night. The odor source was a small patch of krill about 0.5m2.

The simulation for odor dispersion of pyrazine indicates that petrels may be able to detect this component from 2.5 to 12 kilometers from its source, depending upon which level of detection threshold is assumed (Figure 4). The maximum distance can be achieved at the lowest known sensitivity measured [this study] after a period of 60 minutes. Conservative estimates of 2-3 kilometers are obtained if a detection level of 1 ppm is used (Wenzel and Sieck 1972), and these distances can be achieved in as little as 10 minutes. The predicted active space for the less volatiles fatty acid is no less impressive: 1-5 km after 10 minutes for a threshold of 0.1 ppm and after 60 minutes for a threshold of 0.01 ppm, respectively. These predictions are consistent with anecdotal field observations which report petrels "appearing from nowhere" after jettison of offal from ships (Bent 1963). These distances would also allow petrels to effectively cover large areas while foraging, thereby increasing their efficiency at locating prey. We are currently attempting to determine the physical constants of other components of krill.

Determining the active space for krill is more complex than simulating dispersion of component volatiles. At the extremes, petrels may respond to prey odors in one of two ways: analytically or synthetically. In the latter case, the relative concentrations of components in a mixture is important for behavioral responding. Researchers in insect pheromonal biology have long appreciated this fact (Bell and Carde 1984). Interpretation of odor quality (i.e., identity) may vary as a function of odor concentration. For example, in humans, high concentrations of geosmin takes on the odor of musty basements or soil, while at lower concentrations the same odor is identified as beets. If the synthesis hypothesis of odor

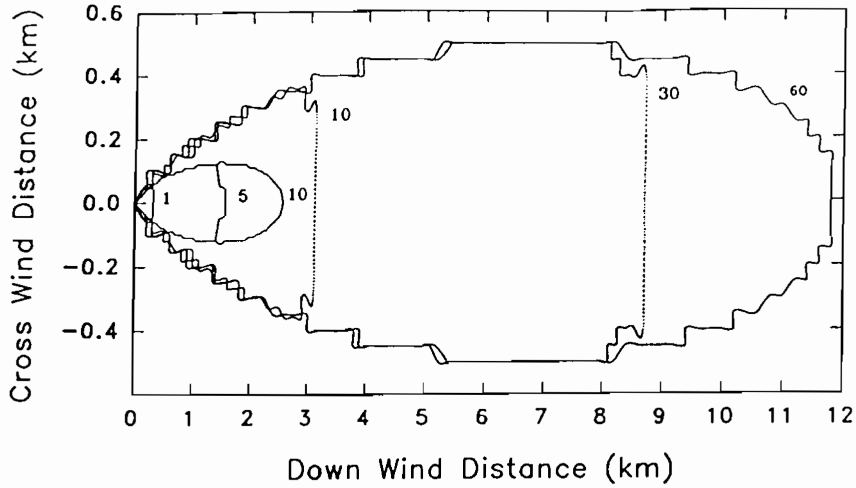

Figure 4. An example of odor dispersion of pyrazine. The odor active space is depicted as an isopleth for a threhsolds of 0.1 ppm (solid lines, smaller dispersion distance) and 0.01 ppm (dotted lines and larger dispersion distance) downwind and crosswind.

quality is correct then, in the case of foraging petrels, the ability to identify the contents of an odor plume will be a function of distance from the source and the evaporation rates of the salient components of the prey odor mixture. Thus, even though individuals components may be above threshold, the distance at which an odor is identified and tracked may be less because the ratios will change as a function of distance from the source, and by implication alter the perception of the odor (Figure 5).

Alternatively, if the odors were interpreted analytically the nature of the odor plume would convey a great deal of information. The trend for the field data suggests that the whole odor fraction is the most attractive. However, rates of attractiveness for carboxylic acid fractions were also high. Carboxylic acids would generally be the least volatile of the fractions and in combination with the higher thresholds, this fraction would have the most restricted active space. When carboxylic acids are encountered, active searching behavior is initiated, presumably because the prey items are reasonably near. This is the behavior most readily detected via the current observation strategy. Orientation to the more volatile amine components would most likely be the best cue for initial orientation because these compounds would disperse most rapidly to great distances at levels within the detection ability of foraging birds. Because this cue may be used as a long distance cue, the circling or target approach criterion used in this study may have underestimated the attractiveness of the cue.

We continue to refine the threshold data and the simulations of odor dispersion. We also are simulating odor dispersion for organic slicks remaining near the surface once the prey have left. Comparing such simulations against steady state odor dispersion simulations may reveal whether it is possible to determine the probability of prey absence from a distance, even though organic volatiles are still present in odor plumes.

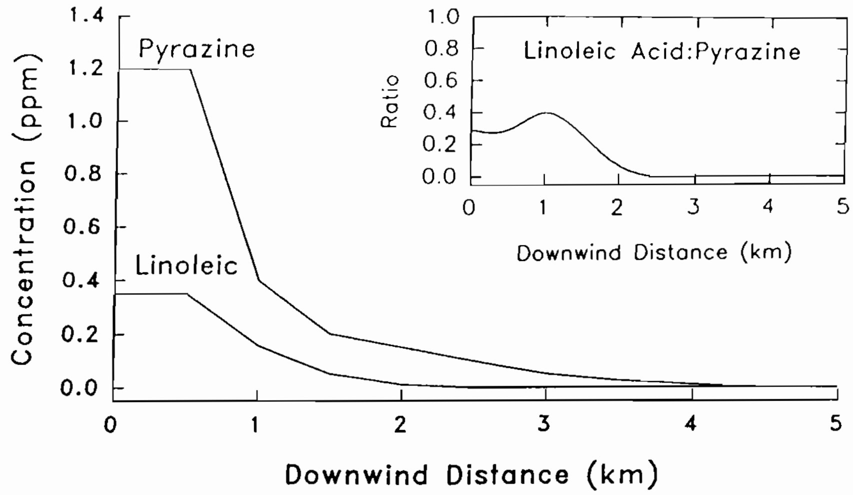

Figure 5. The downwind concentration profiles for pyrazine (solid) and linolenic acid (dotted) as a function of distance from the source. The inset depicts the linolenic acid to pyrazine ratio as a function of distance from the source.

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REFERENCES

Bang, B.G. and Wenzel, B.M. 1986. Nasal cavity and olfactory system. Pl. 195-225 in Form and function in birds, vol. 3 (A.S. King and J. McLelland, Eds.). London, Academic Press.

Bell, W.J. and Carde, R.T. 1984. Chemical ecology of insects. Sunderland, MA, Sinauer Associates, Inc.

Bent, A.C. 1963. Petrels and pelicans and their allies. New York, Dover.

Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California current. Limnol. Oceanogr. 12:451-483.

Brown, R.G.B. 1980. Seabirds as marine animals. Pp 1-39 in Behavior of marine animals. vol. 4, Marine birds (J. Burger, B.L. Olla and H.E. Winn, Eds). New York, Plenum Press.

Clark, L. 1991. Odor detection thresholds in tree swallows and cedar waxwings. Auk 108:177-180.

Clark, L. and Mason, J.R. 1989. Sensitivity of brown-headed cowbirds to volatiles. Condor 91:922-932.

Clark, L. and Smeraski, C.A. 1990. Seasonal shifts in odor acuity by starlings. J. Exp. Zool. 177:673-680.

Everson, I. 1984. Marine Zooplankton. in Pp.463-490. Antarctic Ecology vol. 2, R.M. Laws (Ed.) New York, Academic Press.

Fleischer, M.T. 1980. Spills: an evaportation/air dispersion model for chemical spills. U.S. Department of Commerce, National Technical Information Service PB83-109470.

Grubb, T.C. 1972. Smell and foraging in shearwaters and petrels. Nature, Lond. 237:404-405.

Healy, S. and Guilford, T. 1990. Olfactory bulb size and nocturnality in birds. Evolution.

Hutchison, L.V. and Wenzel, B.M. 1980. Olfactory guidance in foraging by Procellariiformes. Condor 82:314-319.

Kawaguchi, K. 1969. [Diurnal vertical migration of macronektonic fish in the western North Pacific]. Bull Plankton Soc. Japan 16:63-66.

Kubtoa, K., Uchida, C. Kurosawa, K., Komuro, A. and Kobayashi, A. 1989. Identification and formation of characteristic volatile compounds from cooked shrimp. Pp 376-385. in Thermal generation of aromas (T.H. Parliment, R.J. McGorrin, and C.-T. Ho, Eds). ACS Sym. Ser. 409, Wash. D.C.

Kubota, K. and Kobayashi, A. 1988. Identification of unknown methyl ketones in volatile flavor components from cooked small shrimp. J. Agric. Food Chem. 36:121-123.

Lequette, B., Verheyden, C. and Jouventin, P. 1989. Olfaction in subantarctic seabirds: its phylogenetic and ecological significance. Condor 91:732-735.

Mozell, M.M., Sheehe, P.R., Swieck, S.W.,Jr., Kurtz, D.B. and Hornung, D.E. 1984. A parametric study of the stimulation variables affecting the magnitude of the olfactory nerve response. J. Gen. Physiol. 83:233-267.

Murano, M. Marumo, R., Nemoto, T. and Aizawa, Y. 1976. Vertical distribution of biomass of plankton and micronekton in Kuroshio water off central Japan. Bull. Plankton Soc. Japan 23:1-12.

Reid, R.C., Prausnitz, J.M. and Poling, B.E. 1986. The properties of gases and liquids. New York. McGraw Hill.

Sekiguchi, H. 1975. Seasonal and ontogenetic vertical migrations in some common copepods in the norther region of the North Pacific. Bull. Fac. Fish., Mie Univ. 2:29-38.

Shallenberger, R.J. 1973. Breeding biology, homing behavior and communication patterns of the wedged-tailed shearwater Puffinus pacificus. Doctoral Dissertation, University of California, Los Angeles.

Smith, S.A. and Paselk, R.A. 1986. Olfactory sensitivity of the turkey vulture (Cathartes aura) to three carrion-associated odorants. Auk 103:586-592.

Waldvogel, J.A. 1987. Olfactory navigation in homing pigeons: are the current models atmospherically realistic? Auk 104:369-379.

Watanuki, Y. 1985. Food of breeding Leach's storm petrels (Oceanodroma leucorhoa). Auk 102:884-886.

Wenzel, B.M. and Sieck, M.H. 1972. Olfactory perception and bulbar electrical activity in several avian species. Physiol. Behav. 9:287-293.